



**REVIEW**

# Halotolerant PGPR at the Soil–Plant–Microbiome Interface: Microbial Strategies to Enhance Crop Adaptation to Salinity

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**ABSTRACT:** Global climate change has intensified drought and soil salinization, posing serious threats to crop productivity and ecosystem stability. Traditional physical and chemical reclamation methods are often expensive, energy-intensive, and unsustainable. In contrast, halotolerant plant growth-promoting rhizobacteria (HT-PGPR) have emerged as a promising, eco-friendly strategy to address extreme climate change-induced land salinization. HT-PGPR enhance plant tolerance by regulating osmotic balance, ion homeostasis, antioxidant defense, and phytohormone signaling. Current evidence for these effects is largely based on greenhouse pot and microcosm studies, while their validation in field experiments remain limited. In addition, HT-PGPR can improve nutrient availability through nitrogen fixation, phosphorus and potassium solubilization, and siderophore production. This review synthesizes recent advances in the physiological and molecular mechanisms underlying HT-PGPR-mediated stress alleviation, evaluates their performance in well-controlled greenhouse experiments and field applications, and outlines key criteria for strain selection. However, the translation of controlled-environment benefits into consistent field performance remains challenging, due to factors including inoculated microbial survival under fluctuating edaphic conditions, competitive interactions with native soil microbiota, and spatiotemporal variability in climate. Furthermore, we explore emerging innovative approaches such as AI-assisted design of synthetic microbial community for the remediation of saline-alkaline soils. Integrating HT-PGPR into sustainable management practices holds substantial potential for improving crop adaptation and productivity in saline environments under a changing climate.

**KEYWORDS:** Plant growth-promoting rhizobacteria; salt stress; climate change; soil bioremediation; soil remediation

## 1 Introduction

### 1.1 Global Soil Salinization

Soil salinization poses a serious global threat to agricultural sustainability. Recent studies report that salinization affects more than 1 billion hectares of land worldwide, with approximately 76 million hectares attributed to human activities [1,2]. According to the Food and Agriculture Organization (FAO), approximately 20% of irrigated land globally is currently affected by salinity, with salt-affected soils posing a growing threat to global agricultural productivity [3]. The total area of salt-affected land continues to expand globally, driven by poor irrigation practices and climate change, based on FAO global assessments and peer-reviewed analyses [2,4,5]. In China, saline-alkali soils cover more than 90 million hectares, primarily distributed across the northeastern, northwestern, northern, and coastal regions [6]. With the increasing

severity of extreme climate events, soil salinization is expected to intensify, underscoring the urgent need for cost-effective, environmentally friendly, and sustainable reclamation strategies.

### ***1.2 Limitations of Conventional Reclamation Methods***

Conventional approaches for saline soil reclamation, including physical leaching and chemical amendments such as gypsum, can temporarily lower soil salinity but suffer from several major limitations [7]. First, their high water demand makes them impractical in arid and semi-arid regions where freshwater resources are already scarce [4]. In addition, repeated application of chemical amendments may disturb soil nutrient balance and health, and over time induce soil compaction, structural degradation, and a decline in microbial activity [8]. These methods are also economically unsustainable due to the substantial input costs associated with large-scale implementation [9]. Moreover, conventional practices mainly offer short-term relief without addressing the underlying drivers of salinization, often resulting in salt re-accumulation after reclamation [10]. Critically, such approaches neglect the restoration of soil ecological integrity, failing to recover native biodiversity, functional microbial communities, and essential ecosystem processes [11].

In contrast, biological approaches, particularly those based on halotolerant plant growth-promoting rhizobacteria (HT-PGPR), offer a more sustainable and cost-effective alternative. HT-PGPR improve soil health and plant productivity by modulating microbial community composition and function in the soil [12,13]. Therefore, future reclamation efforts should increasingly emphasize microbial and biological restoration techniques to achieve both ecosystem recovery and sustainable agricultural development.

### ***1.3 Microbial Approaches for Saline Soil Rehabilitation: The Role of HT-PGPR***

Microorganisms, especially HT-PGPR, have demonstrated substantial potential in mitigating salt stress and enhancing plant performance in saline environments. HT-PGPR promote plant growth through multiple, well-documented mechanisms, including the synthesis of osmoprotectants, 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity and phytohormone production [7]. As a biological approach, microbial inoculation offers several advantages, such as low cost, high efficiency, and strong environmental compatibility, making it highly aligned with the principles of sustainable agriculture [9]. Beyond direct plant physiological modulation, HT-PGPR can restructure rhizosphere microbial communities, stimulate root system development, and enhance overall plant adaptability to saline stress [14]. These microorganisms also contribute to soil nutrient availability through biological nitrogen fixation, phosphate and potassium solubilization, and siderophore production, thereby supporting nutrient acquisition under salinized conditions [7]. Insights into the metabolic pathways and molecular mechanisms underpinning HT-PGPR function under salt stress provide a mechanistic foundation for developing new bio-mediated reclamation technologies [10]. Research on plant-microbe interactions further elucidates how HT-PGPR influence root morphology, ion homeostasis, and stress-related physiological processes to improve plant salt tolerance [14]. The application of such microbial inoculants not only but also enhances crop yield and quality, delivering significant agronomic and ecological benefits [9].

In summary, microorganisms represent a powerful and ecologically sound tool for mitigating salt stress and rehabilitating saline soils. However, the potential of microbial-based approaches remains far from fully realized, and thus future understanding of the synergistic interactions between HT-PGPR and other beneficial microbes, and advancing the development of high-efficiency synthetic microbial consortia for soil restoration and sustainable agricultural production are necessary [7]. A deeper understanding of microbial metabolic and molecular mechanisms under salt stress will further accelerate the design of next-generation bioremediation strategies. Accordingly, this review summarizes the physiological,

biochemical, and microbial mechanisms through which HT-PGPR enhance plant salt tolerance, evaluates their practical applications in saline soil restoration, and highlights critical research gaps that must be addressed to advance their use in sustainable agriculture.

## 2 Mechanisms of Plant Salt Tolerance Mediated by HT-PGPR

### 2.1 Physiological and Biochemical Mechanisms

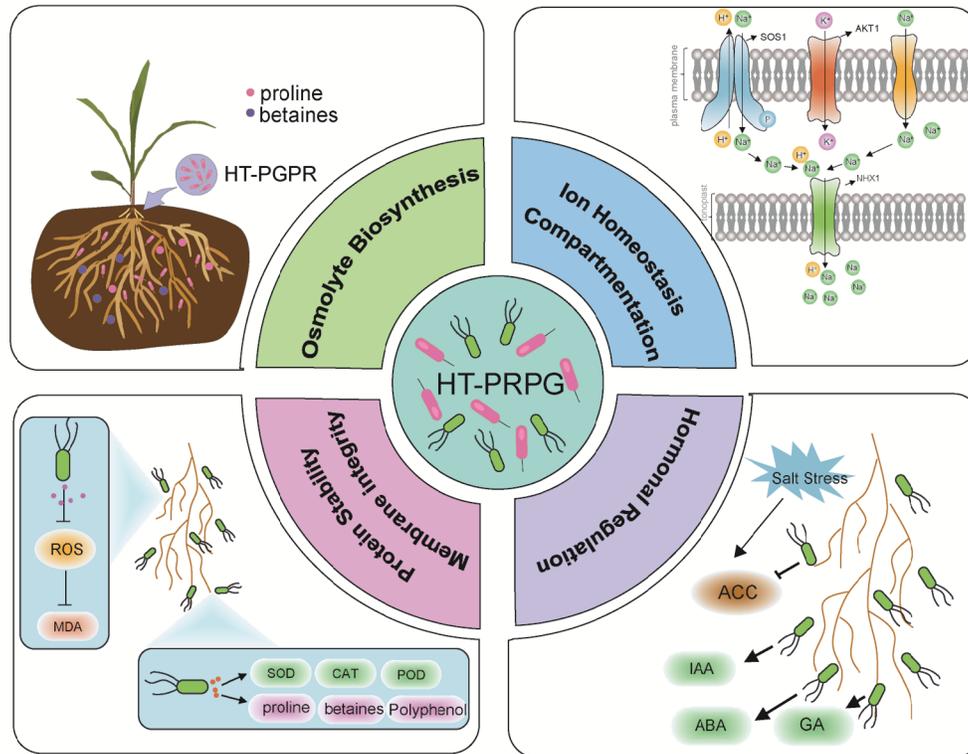
#### 2.1.1 Osmotic Adjustment

HT-PGPR enhance plant salt tolerance by regulating osmolyte biosynthesis pathways in host plants. Proline, one of the most prominent osmoprotectants, shows a context-dependent regulatory pattern shaped by specific plant-microbe interactions. Inoculation with ACC deaminase-producing strains such as *Bacillus megaterium* UPMR2 or *Enterobacter* sp. UPMR18 upregulates proline biosynthetic genes and enhances nutrient uptake, resulting in elevated proline accumulation in salt-stressed okra seedlings [15]. In contrast, inoculation of tomato with *Bacillus megaterium* CJLC2 under 200 mM NaCl stress reduced leaf proline content by 21-33% compared to stressed controls in a greenhouse pot experiment [16].

Other osmolytes, such as betaines and trehalose, also play vital roles in osmotic regulation (Fig. 1). Co-inoculation with *Pseudomonas pseudoalcaligenes* and *Bacillus pumilus* markedly increases betaine-type quaternary ammonium compounds in rice leaves, helping stabilize photosystem II proteins and maintain oxygen evolution in a greenhouse experiment under 43 mM NaCl conditions [15,17]. Trehalose functions as a molecular stabilizer that protects cellular proteins by replacing water molecules and preventing denaturation under osmotic and thermal stress [18]. Notably, many HT-PGPR can synthesize osmolytes more rapidly and efficiently than their plant hosts. For example, strain *Bacillus zhangzhouensis* increases soluble sugar concentrations in maize leaves by 109%, a response consistent with the presence of six proline-related biosynthetic genes identified in its genome [19]. Together, these compatible solutes form a “molecular shield” that preserves cellular osmotic balance, maintains macromolecular stability, and supports enzymatic function under saline conditions. It is important to recognize, however, that osmolyte-mediated responses vary substantially among different plant-microbe combinations, reflecting both microbial genetic diversity and species-specific plant salt tolerance strategies.

#### 2.1.2 Ion Homeostasis and Compartmentation

Laboratory and greenhouse studies indicate that HT-PGPR can contribute to the reestablishment of ion homeostasis in plants, often associated with the modulation of host plant genes encoding  $\text{Na}^+/\text{H}^+$  antiporters such as *SOS1* and *NHX1* (Fig. 1) [5,20]. At the transcriptional level, microbes influence these transport processes. For example, at 200 mM NaCl level, inoculation of *Kocuria rhizophila* upregulates maize *ZmHKT1* and *ZmNHX1/2/3* gene expression in a greenhouse pot experiment, thereby enhancing  $\text{K}^+$  uptake and  $\text{Na}^+$  exclusion [21]. Volatile organic compounds (VOCs) emitted by *Bacillus amyloliquefaciens* FZB42 induce *NHX1* and *HKT1* expression in *Arabidopsis*, resulting in reduced  $\text{Na}^+$  accumulation [22]. Collectively, microbial treatments have been shown to be associated with the upregulation of ion transporter genes (e.g., *HKT1*, *NHX1*) in model systems, which correlates with improved ion balance [5,21,22]. It is important to note that such upregulation may entail metabolic costs for the plant, as energy and resources are diverted to transporter protein synthesis and ion pumping. Moreover, exopolysaccharides (EPS) secreted by PGPR can bind  $\text{Na}^+$  ions in the rhizosphere, acting as an “ion trap” to restrict  $\text{Na}^+$  translocation into roots [23].



**Figure 1:** Biochemical and physiological responses of plant to salt stress mediated by halotolerant plant growth-promoting bacteria (HT-PGPB). HT-PGPB enhance plant tolerance by promoting osmolyte accumulation, maintaining ion homeostasis through selective uptake and exclusion, stabilizing cellular membranes and proteins, and modulating key phytohormone signaling pathways.

These mechanisms maintain a low cytosolic  $\text{Na}^+/\text{K}^+$  ratio, preserving enzyme function and membrane stability under salinity stress. Species-specific adaptations are evident: halophytes like *Salicornia bigelovii* enhance vacuolar  $\text{Na}^+$  sequestration with increasing salinity, as demonstrated by comparing plants grown in a greenhouse under 200 mM NaCl versus 5 mM NaCl conditions [24], whereas glycophytes rely more heavily on *HKT1*-mediated  $\text{Na}^+$  recirculation and exclusion from shoots [25]. Understanding the specificity of microbial regulation in plant ion transport networks will be essential for designing precision bioinoculant strategies.

### 2.1.3 Membrane Integrity and Protein Stability

HT-PGPR also protect plant cells from osmotic and oxidative damage by stabilizing cellular membranes and proteins. Salt stress disrupts reactive oxygen species (ROS) homeostasis, leading to lipid peroxidation and malondialdehyde (MDA) accumulation [15]. Inoculation with *Pantoea dispersa* or *Enterococcus faecium* significantly reduced MDA levels in mung bean leaves subjected to salt stress (50 and 100 mM NaCl) in a greenhouse trial, while meta-analyses show PGPR treatments reduce MDA accumulation by 23–24% across tolerant and sensitive plants [26]. The protection arises from coordinated activation of enzymatic (SOD, POD, CAT) and non-enzymatic (proline, betaine, polyphenols) antioxidant systems. For example, *Dietzia natronolimnaea* STR1, under saline stress conditions (e.g., 100 mM NaCl in hydroponic culture or 150 mM NaCl in soil pot experiments), enhanced the activities and transcript levels of SOD, POD, and CAT

in wheat leaves [27]. Similarly, *Bacillus cereus* Pb25 promoted proline accumulation in mung bean, whereas *Pseudomonas pseudoalcaligenes* produced substantial quantities of glycine-betaine in rice seedlings [17,28].

Beyond antioxidant defenses, microbial inoculation also modulates aquaporins and ion transporter expression to maintain cellular homeostasis. In a potted experiment under 100 mM NaCl salt stress, *Bacillus* spp. upregulates aquaporin genes *LePIP1*, *LeAQP2*, and *LeTRAMP* in tomato leaves, enhancing water transport while enhancing *LeNHX1* and *tomPRO2*, which contributed to reduced ion leakage and improved salt tolerance [16]. Genome analysis of *Bacillus velezensis* and *Bacillus zhangzhouensis* strains reveal catalase and Na<sup>+</sup> efflux genes consistent with these physiological effects [19]. Collectively, these responses constitute a microbial-induced “molecular chaperone” network maintaining redox balance, membrane fluidity, and protein conformation, thereby enhancing plant resilience under salinity stress.

#### 2.1.4 Hormonal Regulation

HT-PGPR modulate phytohormone signaling networks by integrating auxin, ethylene, cytokinin, and gibberellin pathways to coordinate plant responses to salt stress. Salinity typically suppresses auxin biosynthesis; however, *Pseudomonas* and *Bacillus* species can synthesize indole-3-acetic acid (IAA) via the tryptophan-dependent pathway, enhancing root surface area and promoting lateral root formation in soybean [29]. Similarly, strain *Bacillus zhangzhouensis* synthesized IAA, promoting maize root growth and raising the K<sup>+</sup>/Na<sup>+</sup> ratio to 1.98 under salt stress [16]. Notably, the effect of microbial IAA is often dose-dependent; for example, optimal root promotion in *Arabidopsis* was observed at specific IAA concentrations produced by *Pseudomonas* sp., while higher concentrations could be inhibitory [29].

Microbes containing ACC deaminase, such as *Pseudomonas putida*, degrade the ethylene precursor ACC and reduce ethylene accumulation by 30-50% [18]. *Bacillus megaterium* CJLC2 decreases ethylene emission in tomato by 32% [14]. In addition, cytokinins secreted by *Bacillus amyloliquefaciens* B1619 delay leaf senescence and cooperate with gibberellins to regulate stomatal conductance and photosynthetic activity [30]. Hormonal crosstalk is highly dose- and context-dependent, e.g., low IAA promotes root hair development, whereas excessive IAA inhibits primary root elongation [31]. Deciphering the spatial and temporal architecture of microbial hormone regulation will be essential for moving from correlative observations to a mechanistic framework capable of guiding targeted manipulation of plant stress-response networks.

## 2.2 Molecular Pathways: Antioxidant and Signal Transduction Networks

HT-PGPR enhance plant salt tolerance by coordinating ROS homeostasis and activating multi-tiered signaling cascades. Salt stress disrupts redox equilibrium, leading to the accumulation of superoxide (O<sub>2</sub><sup>-</sup>) and hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>). In wheat, inoculation with *Dietzia natronolimnaea* STR1 markedly elevated the activities of antioxidant enzymes, including SOD, POD, CAT, APX, GPX, and GR [15]. In parallel, microbial VOCs trigger MAPK cascades that activate transcription factors *DREB2A/B* and *AREB/ABF*, which in turn regulate downstream antioxidant genes via antioxidant response elements and dehydration-responsive elements [18]. H<sub>2</sub>O<sub>2</sub> serves as a “double-edged signal”: at low levels it activates Ca<sup>2+</sup> and CDPK pathways, whereas at high levels it triggers programmed cell death. *Bacillus velezensis*, which carried five catalase-encoding genes, efficiently decomposes H<sub>2</sub>O<sub>2</sub> into H<sub>2</sub>O and O<sub>2</sub>, thereby reducing maize leaf MDA content to 83% of control [19]. Additional microbial metabolites such as acetylcholine and  $\gamma$ -aminobutyric acid analogs further regulate stomatal movement, decreasing ROS production while maintaining photosynthetic efficiency [6].

Together, these processes form a finely tuned “redox-sensing network”, where NADPH oxidase (Rboh) amplifies ROS signaling and the ascorbate-glutathione cycle serves as a redox buffer. Strain-specific regulatory pathways further modulate plant ion homeostasis. For example, *Bacillus velezensis* induces the expression of plant H<sup>+</sup>-PPase, thereby enhancing the vacuolar proton gradient that facilitates Na<sup>+</sup> sequestration [19], while *Arthrobacter protophormiae* synthesizes dimethylsulfoniopropionate (DMSP) to activate jasmonic acid signaling [18]. Decoding receptor-level, cross-kingdom signaling mechanisms between microbes and host plants remains a major frontier for designing precision microbial inoculants.

## 2.3 Nutrient Utilization and Symbiosis

### 2.3.1 Major Elements Availability

HT-PGPR enhance plant nutrient acquisition under salt stress via biological nitrogen fixation, phosphate solubilization, and potassium mobilization. It's reported that in saline-alkali soils, up to 80% of soil phosphorus exists in insoluble mineral forms due to high pH; HT-PGPR release organic acids (e.g., oxalic, citric) to solubilize these forms, thereby improving plant P uptake. *Pseudomonas* inoculation increased fresh weight in cabbage seedlings, and *Bacillus* enhanced tomato P absorption by 48% [32].

*Brevibacterium frigoritolerans*, *Bacillus velezensis*, and *Bacillus zhangzhouensis* strains produced halos on insoluble phosphate and silicate media, increasing maize K<sup>+</sup> content by 34% under 150 mM NaCl [19]. Nitrogen-fixing bacteria such as *Rhizobium* and *Mesorhizobium* establish symbiotic nodules with legumes, while *Azospirillum lipoferum* improved N accumulation and maintained nitrogenase activity under low oxygen microenvironments [15,33]. These nutrient-mobilizing processes often act synergistically; for instance, K-solubilizing bacteria also enhance P release, while N-fixing bacteria facilitate K mineralization through rhizosphere acidification. Moreover, PGPR inoculation increased the K<sup>+</sup>/Na<sup>+</sup> ratio in tomato roots from 0.78 to 1.28 by regulating *HKT1* and *NHX1* expression [19]. Together, these mechanisms optimize nutrient availability and ion balance, reinforcing plant resilience in saline environments.

### 2.3.2 Siderophore Production and Plant Interaction

HT-PGPR produce siderophores that chelate Fe<sup>3+</sup>, enhancing plant iron acquisition under saline conditions [34]. Strains *Bacillus velezensis* and *Bacillus zhangzhouensis* synthesize catecholate-type siderophores encoded by nonribosomal peptide synthetase (NRPS) and fur-regulated gene clusters [19].

Siderophores not only suppress wheat sheath blight by 68% but also increase iron bioavailability. *Arthrobacter protophormiae* inoculation increased Fe content in tomato by 2.3-fold and upregulated *FER* and *FIT* expression [6,35]. *Bacillus* species typically produce bacillibactin-type siderophores, whose biosynthesis correlates positively with salinity levels, while *Pseudomonas* tends to generate pyochelin-type molecules [19]. Fe<sup>3+</sup>-siderophore complexes enter plant cells via YSL transporters, activating transcription factors *FIT1* and *bHLH038*, which regulate *IRT1* and *FRO2* for Fe uptake [36]. Thus, siderophore production integrates microbial iron scavenging with host Fe homeostasis, establishing a cooperative defense-nutrition interface under salt stress.

### 2.3.3 Crop-Specific Applications

HT-PGPR exhibit crop-specific adaptations in enhancing salt tolerance through distinct physiological and molecular pathways. In rice (*Oryza sativa*), co-inoculation with *Pseudomonas pseudoalcaligenes* and *Bacillus pumilus* elevated betaine-type osmolytes and proline accumulation by 2.8-fold under 43 mM salt stress. In wheat (*Triticum aestivum*), *Azospirillum lipoferum* increased N accumulation by 37% while modulating *HKT1* and *AKT1* expression involved in ion homeostasis [17]. In maize (*Zea mays*), multiple

*Bacillus* strains improved growth and antioxidant capacity. *Bacillus tropicalis* increased plant height by 45%, *Fictibacillus arsenicus* enhanced CAT and SOD activities, reducing MDA by 31%, and *Bacillus velezensis* improved both proline content and membrane stability [16]. In legumes, *Rhizobium-Medicago sativa* symbiosis maintained high leghaemoglobin and nitrogenase activity, while *Mesorhizobium* increased nodule numbers by 2.3-fold. *Bacillus subtilis*-*Acacia* interaction boosted nitrate and nitrite reductase activity by 42% [15,37].

These findings highlight that monocots (e.g., rice, wheat) primarily rely on ion regulation, legumes on symbiotic nitrogen fixation, and C4 crops like maize can achieve salt tolerance through integrated antioxidant and osmotic mechanisms [38]. Future work should focus on developing plant-microbe compatibility models to optimize HT-PGPR applications across saline agroecosystems.

### 3 Major Groups of Halotolerant Microorganisms

#### 3.1 Bacteria

Among halotolerant microorganisms, PGPR represent the core functional group, primarily including the genera *Bacillus*, *Pseudomonas*, and *Halomonas*. Representative *Bacillus* species, *B. subtilis*, significantly increased 38.4% and 56.7% in glycine betaine and proline of *Acacia gerrardii* Benth under 200 mM NaCl stress in a greenhouse experiment [39]. *Halomonas* species exhibited remarkable adaptability by switching between halophilic and non-halophilic growth modes, accumulating compatible solutes such as ectoine and hydroxyectoine to maintain osmotic balance [40]. For example, *H. desiderata* and strain STR8 increased proline accumulation in maize leaves by 61% under 500 mM NaCl stress [41].

These bacterial taxa display functional complementarity. *Bacillus* species are efficient phosphate and potassium solubilizers, *Pseudomonas* species excel in siderophore-mediated pathogen suppression, while *Halomonas* specializes in the biosynthesis of organic osmolytes [42]. At the molecular level, bacterial halotolerance is linked to conserved salt-stress operons such as proU (proline transport) and bet (glycine betaine biosynthesis) [43]. Future comparative genomics studies are needed to elucidate the evolutionary trajectories of salt adaptation across genera, providing a theoretical basis for the design of multi-strain, synergistic “microbial consortia” for saline agriculture.

#### 3.2 Fungi (Arbuscular Mycorrhizal Fungi and Endophytic Fungi)

Halotolerant fungi, primarily arbuscular mycorrhizal fungi (AMF) and endophytic fungi, can enhance plant salt tolerance through symbiotic interactions and extensive hyphal networks. AMF species such as *Funneliformis mosseae*, *Rhizophagus intraradices*, and *Claroideoglossum etunicatum* facilitate nutrient and water transport, improving Na<sup>+</sup> efflux and ionic homeostasis. For instance, AMF inoculation increased Na<sup>+</sup> extrusion efficiency by 47% and raised the K<sup>+</sup>/Na<sup>+</sup> ratio to 2.8 in rice roots [44]. This effect is closely associated with the upregulation of aquaporin genes (*PIP2;1* and *TIP4;1*), enabling alfalfa leaves to maintain 78% relative water content under 200 mM NaCl stress [45]. The endophytic fungus *Serendipita indica* mitigates salt-induced oxidative stress by activating the host antioxidant system, enhancing SOD and POD activities by 1.9-fold and 2.3-fold, respectively, while reducing MDA content by 41% in wheat leaves [46]. Synergistic AMF-PGPR interactions further enhance tolerance. Co-inoculation of *F. mosseae* and *Methylobacterium oryzae* CBMB20 increased maize root colonization by 68%, reduced proline accumulation, and elevated glycine betaine levels, suggesting a shift from a damage-repair to a pre-adaptive osmotic regulation strategy [47]. At the molecular level, AMF secrete effector-like proteins that modulate host gene expression. For example, the SiSSP1 effector interacts with the rice transcription factor *OsTFIIBy* to activate

*OsNHX1*, facilitating vacuolar Na<sup>+</sup> sequestration [45]. These findings underscore fungi as biointerfaces coupling ionic balance, water transport, and host gene regulation under salinity stress.

### 3.3 Archaea (Extremely Halophilic Archaea)

Extremely *Halophilic archaea*, mainly belonging to the Euryarchaeota and Thaumarchaeota phyla, maintain cellular homeostasis under saturated saline conditions through unique cellular adaptations. They express high-affinity K<sup>+</sup> transporters (e.g., KdpATPase) and produce acidic, halostable proteins (such as ferredoxins and ribosomal proteins) to maintain enzymatic function. For instance, *Halobacterium* retains enzymatic stability even at 4.5 mM NaCl [48]. Their membranes, composed of diether lipids, form a molecular shield with superior hydrolytic resistance compared to bacterial ester membranes, enabling *Methanococcus* species to maintain membrane integrity under 15% salinity fluctuation [48].

Metabolic complementarity between archaea and bacteria has also been observed in many previous studies. For example, members of the Halanaerobiales convert bacterial metabolites into osmoprotectants; when co-cultured with *Halomonas*, glycerol degradation efficiency increases 3.2-fold [49]. Inoculation with the halophilic archaeon *Halolamina pelagica* CDK2 significantly enhances plant growth under saline conditions, increasing grain yield by 30-50% and improving total protein and chlorophyll content, while reducing antioxidant enzyme activity [50].

However, archaea represent only a small fraction of halotolerant microorganism studies, and direct evidence of plant-archaea interactions remains limited [51]. Addressing the challenges of archaeal cultivation and integrating 16S sequencing with haloproteomics will be essential for identifying novel compatible solutes (e.g., ectoine derivatives, glycine betaine analogs) with potential applications in developing salt-tolerant crops. Such research could ultimately bridge fundamental gaps between prokaryotic and eukaryotic strategies of salt adaptation.

Collectively, these microbial groups exhibit distinct yet functionally convergent strategies to enhance plant performance under salinity. A comparative overview of representative taxa, mechanistic traits, and plant physiological outcomes is presented in Table 1.

**Table 1:** Representative halotolerant microorganisms, their salt-tolerance mechanisms, and associated plant responses.

Functional Category	Representative Strains/Genera	Functional Description	References
Hormonal Regulation and Signal Transduction	<i>Enterobacter cloacae</i> , <i>Dietzia natronolimnaea</i> , <i>Pseudomonas</i> PS01	Modify ethylene and auxin levels; induce expression of <i>TaMYB</i> and <i>TaWRKY</i> genes; regulate stress-responsive genes; activate <i>LOX2</i> and jasmonic acid (JA) signaling pathways	Yaish et al., 2015 [52]; Bharti et al., 2016 [27]; Chu et al 2019 [53]
Antioxidant Defense and Oxidative Stress Mitigation	<i>Arthrobacter</i> sp., <i>Bacillus</i> sp., <i>Bacillus pumilus</i> AM11, <i>Exiguobacterium</i> sp. AM25, <i>Bacillus fortis</i> SSB21	Increase proline content and total biomass; enhance glutathione, catalase, and peroxidase activities; decrease ROS accumulation	Sziderics et al., 2007 [54]; Ali et al., 2017 [55]; Yasin et al., 2018 [56]
Ion Homeostasis and Osmotic Regulation	<i>Bacillus subtilis</i> , <i>Variovorax paradoxus</i> , <i>Planococcus rifetoensis</i> , <i>Pseudomonas migulae</i> 8R6, <i>Pseudomonas fluorescens</i> YSs6, <i>Kocuria rhizophila</i> Y1	Reduce Na <sup>+</sup> accumulation and ROS production; maintain ionic and osmotic balance through ACC deaminase activity that lowers host ACC levels	Ali et al., 2014 [57]; Hashem et al., 2016 [37]; Zhou et al., 2017 [58]; Li et al., 2020 [21]

**Table 1: Cont.**

Functional Category	Representative Strains/Genera	Functional Description	References
Photosynthesis and Nutrient Metabolism	<i>Halomonas desiderata</i> STR8, <i>Bacillus pumilus</i> AM11, <i>Bacillus cereus</i> Pb25, <i>Exiguobacterium</i> sp. AM25	Enhance photosynthesis and chlorophyll content; solubilize phosphate and improve available soil P; facilitate nutrient absorption Produce biofilms and extracellular polysaccharides; colonize the rhizosphere, improve root architecture and soil phosphorus availability; promote plant growth under stress	Bharti et al., 2014 [59]; Islam et al., 2016 [28]; Ali et al., 2017 [55]
Biofilm Formation and Rhizosphere Colonization	<i>Planococcus rifietoensis</i> , <i>Pseudomonas</i> sp. P34-L, <i>Halomonas</i> sp. Exo1	Induce systemic salt tolerance via transcriptional regulation; emit VOCs that reduce Na <sup>+</sup> accumulation, increase chlorophyll content, and maintain leaf osmotic potential and membrane integrity	Qurashi and Sabri, 2012 [60]; Mukherjee et al., 2019 [23]
Induced Systemic Tolerance	<i>Bacillus amyloliquefaciens</i> FZB42, <i>Bacillus subtilis</i> strain GB03	Fix atmospheric nitrogen, improving nodule formation efficiency in legumes under salt stress; stimulate seed germination under saline conditions	Han et al., 2017 [61]; Liu et al., 2017 [62]
Symbiotic Nitrogen Fixation and Growth Promotion	<i>Burkholderia cepacia</i> , <i>Bradyrhizobium</i> (RA-5), <i>Kocuria rhizophila</i> Y1		Bano et al., 2015 [63]; Li et al., 2020 [21]

## 4 Applications of HT-PGPR in Saline Soil Remediation

### 4.1 Enhancing Crop Salt Stress Tolerance

#### 4.1.1 Field Performance of Wheat (*Dietzia*), Soybean (*Pseudomonas*), and Tomato (*Bacillus*)

HT-PGPR markedly enhance crop salt tolerance and field yield through multi-mechanistic cooperation. Under saline conditions, these microbes optimize plant metabolism by synthesizing osmolytes (e.g., proline, betaine), regulating ion transporter genes (e.g., *HKT* family), and activating antioxidant and systemic defense pathways. In wheat, *Dietzia* inoculation upregulated *TaMYB/TaWRKY* transcription factors, elevated SOD and CAT activities, increased proline accumulation by 47%, and lowered MDA by 20%, leading to a 23% yield increase under salt stress [27]. For instance, inoculation of wheat with *Dietzia natronolimnaea* STR1 in a field trial at a single site resulted in a 23% yield increase under saline conditions [64]; multi-site validation is needed to confirm this effect across diverse environments.

In soybean, *Pseudomonas* strains optimized root architecture by synthesizing IAA while reducing ethylene accumulation through ACC deaminase activity, increasing root surface area by 51%, P uptake by 37%, and biomass gain by 42% in saline fields [7,65]. Similarly, in a greenhouse trial with tomato, inoculation with a *Bacillus subtilis* consortium under 200 mM NaCl resulted in a significant 13.9% increase in fresh biomass weight per plant ( $p < 0.05$ ) compared to the non-inoculated control [66]. Collectively, these studies demonstrate that HT-PGPR act as biological “stress modulators”, engineering robust plant-soil feedback loops that translate molecular benefits into tangible yield gains in saline agroecosystems.

#### 4.1.2 Cross-Crop Applicability

HT-PGPR exhibit broad cross-crop applicability by integrating conserved stress-mitigation pathways with species-specific adaptive responses. Their core mechanisms, osmolyte synthesis, EPS secretion, antioxidant activation, and SOS pathway regulation, provide a universal foundation for mitigating osmotic stress and ion toxicity in diverse crops [7]. Wheat inoculated with *Dietzia* exhibited proline accumulation via *TaMYB/TaWRKY* activation [27]; soybean-*Pseudomonas* interactions decreased ethylene levels and improved P mobilization [65]; and *Bacillus*-treated tomato plants formed EPS-mediated biofilms that restricted Na<sup>+</sup> translocation and improved fruit quality [67].

At the same time, functional specialization enables strain-host matching: *Rhizobium* enhances N fixation in legumes, while *Kushneria* promotes growth of halophytes like *Suaeda salsa* through phosphate solubilization [68,69]. Field and pot studies have reported that HT-PGPR inoculation, often combined with organic amendments, can reduce soil electrical conductivity (EC) (e.g., a field study with wheat showed a 9.4% reduction after one growing season [70]; a greenhouse study with maize reported a 31% decrease in soil EC under the phosphogypsum and bacteria co-inoculation [71]). Thus, the cross-crop versatility of HT-PGPR reflects a modular and scalable functional architecture, supporting their deployment as universal microbial tools in saline agriculture.

### 4.2 Improving Soil Quality and Health

#### 4.2.1 Soil EC and pH Regulation

Beyond enhancing plant resilience, HT-PGPR play vital roles in restoring soil health, particularly in regulating soil EC and pH. By secreting EPS and organic acids, these microbes decrease soluble Na<sup>+</sup> concentrations through cation bridging, hydrogen bonding, and anion adsorption, contributing to 18–35% reductions in EC [7]. Low-molecular-weight acids (e.g., oxalic, citric acids) neutralize alkaline compounds, reducing soil pH from 9.4 to 8.6 [70]. During P solubilization, *Pseudomonas moraviensis* releases H<sup>+</sup> ions that lower soil pH and increase P availability, while *Bacillus cereus* combined with phosphogypsum improves organic matter and dehydrogenase activity [7]. Microbial biofilms act as “natural ion exchangers”, sequestering Na<sup>+</sup> and promoting soil aggregation, porosity, and infiltration [21]. Together, these microbially mediated processes drive a progressive shift toward chemically balanced and biologically active soils, laying the foundation for long-term saline-alkaline land improvement.

#### 4.2.2 Increasing Soil Organic Matter and Nutrient Cycling (N/P/K)

HT-PGPR enhance soil organic matter (SOM) and nutrient cycling through synergistic biochemical pathways. EPS serves as a carbon-rich pool that promotes soil aggregation. For instance, soil microorganisms secreting EPS are important for improving soil aggregates, which are key parameters for sustainable soils. Inoculation of bacteria with high EPS production can significantly improve the stability of soil aggregates, enhance soil fertility and improve soil quality [72–74]. Nitrogen-fixing *Pseudomonas aeruginosa*, combined with organic amendments, significantly increased soil N levels compared with uninoculated controls, while in the P cycle, strains such as *Oceobacillus picturae* and *Bacillus licheniformis* MH48 increase available P by 18–35% [71]. Potassium mobilization occurs via ion exchange and mineral weathering, raising leaf K content by 14% under low-salt and 8% under high-salt conditions [15]. Enhanced soil enzyme activities (dehydrogenase, phosphatase) foster organic matter mineralization and nutrient turnover, generating a positive microbe-soil-nutrient feedback loop [5]. These improvements demonstrate that HT-PGPR serve as

ecological catalysts, accelerating soil nutrient renewal and rebuilding the biogeochemical functionality of saline-degraded systems.

#### 4.2.3 Enhancing Soil Water Retention and Microbial Diversity

HT-PGPR significantly improve soil water retention and microbial diversity through biophysical and ecological mechanisms. EPS produced by strains such as *Alcaligenes latus* and *Pseudomonas aeruginosa* CMG1421 functions as natural hydrogels that enhance aggregate stability and porosity [7,60]. This “bio-sponge effect” increased soil infiltration by 35% and root water potential by 28% [15]. EPS-soil complexes create nutrient-rich microhabitats that support diverse microbial communities, increasing microbial biomass carbon by 67% [7]. *Planococcus rifietoensis* RT4 and *Halomonas variabilis* HT1 significantly enhanced soil aggregation [75]. Enhanced microbial diversity was reflected in higher actinomycete and diazotroph populations, increased dehydrogenase activity, and improved carbon turnover [69]. Notably, biofilm-associated quorum sensing enhances microbial recruitment and stabilizes a root–microbiome mutualistic network, resulting in a 1.8–2.3-unit increase in the Shannon diversity index under salt stress [70]. These coordinated improvements in water dynamics and microbial ecology contribute to building resilient soil microecosystems capable of withstanding combined salinity and drought pressures.

### 4.3 Development of Microbial Bioformulations

#### 4.3.1 Selection Criteria for Halotolerant Strains

Screening of HT-PGPR strains should adopt a multi-parameter evaluation system based on key physiological indicators. EPS yield directly correlates with salt-stress mitigation efficiency; high-yielding strains (e.g., *Halomonas* sp. EX01) can produce EPS accounting for 40–90% of dry biomass under salt stress, forming dense ion-binding matrices that restrict  $\text{Na}^+$  migration toward plant roots [76]. Conversely, an EPS-deficient mutant of *Pantoea alhagi* NX-11 lost antioxidant activity, reinforcing the positive linkage between EPS abundance and oxidative defense [66]. ACC deaminase activity must be verified both genetically and enzymatically. High-performance strains such as *Pseudomonas* sp. UW4 degrade plant ACC into  $\alpha$ -ketobutyrate and ammonia, reducing ethylene accumulation by 35–50% under salt stress [67]. The activity threshold should exceed  $4.8 \mu\text{mol } \alpha\text{-KB mg}^{-1}\text{h}^{-1}$  [65], with gene confirmation using *acdSf3/acdSr3* primers to ensure *acdS* conservation [66]. Biofilm formation, typically quantified via crystal violet staining, represents another essential trait. Biofilm-forming strains such as *Enterobacter cloacae* establish ion-filtering microcolonies within rhizosphere pores, enhancing macroaggregate stability by up to 60% [77]. Collectively, EPS provides the structural scaffold, ACC deaminase maintains the rhizosphere physiological balance, and biofilms strengthen ecological persistence, together forming a “physical-physiological-ecological” triple-protection mechanism [7]. These criteria have guided the industrial development of more than 20 core strains (e.g., *Bacillus amyloliquefaciens*, *Pseudomonas fluorescens*), establishing a robust scientific foundation for selecting HT-PGPR-based bioformulations in saline soil remediation.

#### 4.3.2 Design Principles of Synthetic Microbial Consortia

The rational design of synthetic microbial consortia (SynComs) represents a major step toward improving productivity and remediation efficiency in saline-alkaline soils. SynComs combine strains with complementary halotolerance and growth-promoting functions to form synergistic and resilient communities. Three fundamental principles should be used to guide design: (i) inter-strain interactions, understanding symbiotic, antagonistic, or competitive relationships enables optimized combinations that maximize cooperation and minimize interference [69]; (ii) environmental adaptability, selecting

highly salt-tolerant and stress-adaptive strains ensures survival and colonization under fluctuating saline conditions [71]; and (iii) stability and persistence, optimizing formulation and encapsulation technologies (e.g., microcapsules) helps shield microbes from environmental fluctuations and extend field efficacy [69,70]. Together, these principles underpin the construction of stable, high-performance SynComs that sustainably enhance soil productivity and accelerate saline–alkaline land restoration.

Although these rationally designed SynComs, constructed based on inter-strain synergy, environmental adaptability, and stability principles, may effectively enhance plant salt tolerance and improve soil quality through various mechanisms, their successful field application still faces numerous limitations and challenges. The main bottlenecks include: poor survival and colonization efficiency of introduced strains in complex soil environments (especially under salt stress); intense spatial and nutritional competition with native microbial communities; high heterogeneity of field soil physicochemical properties (such as salinity, pH, and texture); and immature inoculant formulation and delivery technologies, which make it difficult to ensure long-term viability and efficacy of the bacterial cells. These factors lead to inconsistent and unstable growth-promoting and salt-tolerance effects in field applications, which often differ significantly from laboratory results. Future research and application need to focus on developing more environmentally adaptable inoculant formulations (e.g., using nanomaterials, adding protective agents), utilizing microbial community synergies, and conducting targeted design and testing based on specific soil conditions, in order to bridge the gap between experimental research and practical application.

#### *4.3.3 Role and Prospects of Artificial Intelligence (AI) in Designing Halotolerant Microbial Consortia*

The construction of halotolerant PGPR consortia has shifted from empirical screening toward AI-assisted rational design. Artificial intelligence integrates multi-omics datasets, predicts microbial interactions, and optimizes SynCom composition, substantially improving design efficiency, functional predictability, and ecological stability. Machine learning (ML) and deep learning (DL) can integrate metagenomic, metabolomic, and transcriptomic data to identify key functional strains associated with salt tolerance, including genes for compatible solute synthesis (ectoine, betaine), ion homeostasis ( $\text{Na}^+/\text{H}^+$  antiporters), and auxin or quorum-sensing signal production. Feature selection algorithms (e.g., random forest, SVM) can prioritize strains most responsive to salt stress while minimizing redundancy, predicting compatibility and long-term stability within SynComs.

AI-based ecological modeling, using network analysis and Lotka-Volterra dynamics, can anticipate cooperative or competitive interactions, avoiding inhibitory combinations. Dynamic simulations also optimize inoculation order and strain ratios to maintain SynCom stability. In practical applications, AI integrates environmental variables (salinity, pH, moisture) to design location-specific SynComs. Real-time monitoring (fluorescence imaging, qPCR) coupled with DBTL (Design-Build-Test-Learn) cycles enables continuous optimization. Platforms such as BacterAI iteratively refine SynCom performance using automated experimental feedback [78,79]. Moreover, DL-based phenotyping (e.g., CNN analysis of plant images) enables early prediction of plant salt-tolerance responses, facilitating proactive management. While AI-assisted design shows promise for microbial strain selection and SynCom optimization, its application in rhizosphere systems remains nascent and is supported by only limited, proof-of-concept studies. Current models are often trained on greenhouse-derived datasets, making them vulnerable to data bias and limited field transferability [80]. Consequently, AI/ML predictions require rigorous mechanistic validation and field-scale testing before reliable application.

#### 4.4 To What Extent Does the Salinity Gradient Determine Microbial Remediation Potential?

The efficacy of SynComs in ameliorating salt stress is likely not uniform across soil salinity gradients. Theoretical and empirical evidence suggests that their beneficial impacts may be more pronounced in lightly to moderately saline soils, while potentially diminishing in severely saline-alkaline conditions [43]. In light saline soils, the primary constraints on plant growth are often osmotic stress and initial ionic imbalance. Here, PGPR/SynComs can effectively deploy their core mechanisms, such as the production of osmoprotectants (e.g., proline, glycine betaine) [66], ACC deaminase-driven ethylene reduction [71], and moderate enhancement of nutrient solubilization and phytohormone modulation [77]. These interventions can significantly improve seedling establishment, root growth, and overall plant vigor, providing a crucial buffer against the initial salinity shock [64].

However, as salinity intensifies to moderate and severe levels, the extreme osmotic pressure, specific ion toxicity ( $\text{Na}^+$ ,  $\text{Cl}^-$ ), and deteriorated soil physicochemical properties (e.g., high pH, poor structure) exceed the physiological tolerance of many beneficial strains [43,60]. Severe stress reduces microbial survival and colonization, while intense ion toxicity and extreme pH damage microbial enzymes and impair key plant-growth-promoting functions [81]. Although some halotolerant strains exhibit remarkable resilience [9,42], their ability to meaningfully influence plant physiology under such extreme abiotic stress may be substantially curtailed [70].

In summary, while bio-inoculants represent a promising strategy for saline soil remediation, their application might be most effective as a proactive or early-intervention measure in lightly to moderately affected soils, whereas their role in severely degraded lands may be limited unless integrated with other amelioration practices (e.g., organic amendments, physical leaching) [7,82].

### 5 Conclusion and Future Perspectives

HT-PGPR provide a sustainable biological approach for enhancing productivity and ecological restoration in saline soils. By regulating osmotic adjustment, ion homeostasis, and plant hormonal-signaling pathways, HT-PGPR improve plant salt tolerance while reshaping rhizosphere functions. However, field-scale translation remains challenging due to limited adaptability, inconsistent stability, and competition with native microbiota. To overcome these constraints, future research should focus on several key aspects.

(1) **Screening efficient and resilient HT-PGPR strains.** Advanced approaches such as high-throughput sequencing, genome mining, and precision editing can facilitate the discovery of highly adaptable and functionally consistent strains, followed by validation across diverse soil and climatic conditions.

(2) **Developing novel HT-PGPR formulations and inoculation technologies.** Integrating modern biotechnology with material science may enable innovative encapsulation or carrier technologies that improve microbial survival, rhizosphere colonization, and long-term persistence in saline environments.

(3) **Enhancing AI-assisted construction of SynComs.** Building specialized datasets for halotolerant microbes and applying artificial intelligence algorithms can facilitate tailored SynComs optimized for specific salinity-alkalinity contexts.

Overall, HT-PGPR represent an eco-friendly and promising solution for saline soil remediation and sustainable agriculture. With the integration of microbial ecology, systems biology, and intelligent design technologies, their applications are expected to evolve from experimental validation toward large-scale, data-driven, and intelligent agricultural practices.

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